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Research Article

Do native trees support epiphytic bryophytes diversity better than nonnatives?

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Abstract

The influence of nonnative angiosperm trees on epiphytic bryophyte diversity is a major gap in invasion ecology. Two prominent invasive species, *Acer negundo* and *Prunus cerasifera*, are expanding rapidly into temperate forests, and, therefore may have the potential to impact epiphytic bryophyte communities. In this study, we compared the effects of tree diameter at breast height (*DBH*) on epiphytic bryophyte diversity among two native (*Quercus robur* and *Acer platanoides*) and two invasive (*A. negundo* and *P. cerasifera*) tree hosts, and assessed the ecological mechanisms shaping the community assembly of bryophytes colonizing their bark. We conducted our study in the surroundings of the Białowieża National Park by surveying epiphytes inhabiting the studied tree species, with 25 individuals per tree species selected, each varying in *DBH*. Using ordination and linear regression methods, we found that interspecific competition could play a similarly important role in shaping the assembly processes of bryophyte communities on *A. platanoides* and *A. negundo*, as indicated by a negative relationship between *DBH* and functional diversity metrics. This pattern corresponds with the highest mean water capacity of bark observed for *A. negundo*, as well as the relatively higher mean bark pH of *A. negundo* compared to native tree hosts – *A. platanoides* and *Q. robur*. Larger *P. cerasifera* trees may support more competitive bryophytes, as revealed by the negative relationship between *DBH* and functional richness. However, habitat filtering appears to play a prominent role in community assembly on *P. cerasifera*, as evidenced by its bark's lowest mean pH and water capacity among the surveyed phorophytes, and by increasing the proportion of pioneer and light-demanding epiphytes with tree size. For *Q. robur*, with close-to-neutral bark pH and low water capacity, the influence of interspecific competition on bryophyte community assembly across the *DBH* gradient was less pronounced compared to other phorophytes, likely due to the slower development of suitable microhabitats for epiphyte colonization. The ability of nonnative *A. negundo* and *P. cerasifera* to support functionally diverse bryophyte communities, similar to native hosts, highlights their potential as key hosts for restoring and persistence of epiphytic biota in tree plantations and urban ecosystems. Our study offers new insights into the impact of invasive trees on a largely underexplored group of dependent organisms, expanding the functional and phylogenetic scope of nonnative trees assessed for impact on bryophytes.

Key words: *Acer negundo*, bryophytes, epiphytes, functional diversity, nonnative trees, phorophyte, *Prunus cerasifera*

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Introduction

In the temperate climate zone, epiphytic bryophytes form a crucial ecological group colonizing the bark of living trees. Many of these species are highly sensitive to environmental changes and are considered threatened (Wierzcholska et al. 2020; Collart et al. 2023). Owing to their unique physiological and biological characteristics, epiphytic bryophytes serve as key indicators of environmental change (Proctor 2011; Slack 2011). The longevity of their tree hosts is a critical factor influencing the distribution and persistence of this functional group (Emrich et al. 2025). As a highly dependent group, they are influenced by multiple factors, e.g., bark pH, surface texture, water-holding capacity, tree species identity, bark fissuring, the amount of light reaching the trunk or age of the tree (Barkman 1958). Additionally, the surrounding environmental conditions play a crucial role in shaping their distribution and diversity (Patiño and González-Mancebo 2011). Their ability to colonise various substrates and their sensitivity to environmental changes make them excellent indicators of habitat suitability and stability (Baker et al. 2018; Fojcik et al. 2019). This adaptive capacity is crucial for assessing their potential for colonisation across diverse substrates.

As forest specialists, epiphytic bryophytes play several essential roles in forest ecosystem functioning. They possess a remarkable ability to intercept and retain rainwater, thereby contributing to the forest water cycle. Additionally, epiphytes provide habitats for various taxonomical groups of organisms (Zhao et al. 2020). Their ecological preferences are closely linked to specific microhabitats, such as the bark characteristics of living trees and their light requirements. Additionally, as poikilohydric organisms, they exhibit a pronounced dependence on atmospheric humidity, making them highly responsive to environmental fluctuations (Glime 2017). This physiological sensitivity allows them to serve as bioindicators of ecosystem stability and transformation (Mežaka et al. 2012; Wierzcholska et al. 2020; Wierzcholska et al. 2024a).

The relationship between the phorophyte species and bryophyte assemblages is a well-established and extensively studied phenomenon in temperate forests (Barkman 1958; Király and Ódor 2010). The limited research has directly investigated the impact of invasive trees on epiphytic bryophytes, thus, studies on nonnative tree species offer valuable insights (Collart et al. 2023). Some nonnative trees support diverse bryophyte communities, although their ecological roles often differ from those of native trees (Jagodziński et al. 2018; Ennos et al. 2019; Mitchell et al. 2021; Bury and Dyderski 2025). In general, the impact of nonnative tree species on bryophytes was ten times lower studied than on vascular plants (Wohlgemuth et al. 2022), indicating most frequently neither positive nor negative effects. Most of the evidence provided by the cited review focused on epigeic bryophytes while omitting epiphytes.

There are only a few studies analysing the effects of nonnative trees on epiphytic bryophytes. In managed forests nonnative *Quercus rubra* fails to replace native congenerics as phorophyte supporting epiphytic flora (Gustafsson et al. 2024). However, contrasting findings from post-agricultural forests suggest that *Q. rubra* may facilitate bryophyte recolonisation in these landscapes. Although *Q. rubra* contributes to ecosystem dynamics, its adverse impact on ground flora, including bryophytes, raises concerns about its overall role in maintaining native biodiversity (Woziwoda et al. 2017). Research conducted in novel ecosystems, such as spoil heaps, suggests that certain nonnative trees like *Robinia pseudoacacia* and *Q. rubra* may provide a refuge for epiphytic flora, whereas their negative

impact on the understory bryophytes has also been documented (Jagodziński et al. 2018). Studies in urban parks and urban forests further suggest that nonnative trees host distinct epiphytic floras, markedly different from those associated with native tree species (Fudali and Szymanowski 2019). In particular, two alien phorophytes, *Acer negundo* and *Populus ×canadensis*, revealed the highest similarity in bryophyte species composition to each other while differing significantly from both native and other nonnative phorophytes. Notably, no exclusive bryophyte species were found on their trunks. Similarly, another study has demonstrated that alien *Fraxinus pennsylvanica* does not provide a superior habitat for epiphytes in terms of species diversity (Dittrich et al. 2021). However, all these studies assessed only the taxonomic diversity of bryophytes.

The influence of trees on the taxonomic diversity of epiphytic bryophytes is relatively well understood, particularly concerning native phorophyte species (Wierzcholska et al. 2018; Wierzcholska et al. 2024b), however functional diversity (*FD*) represents a novel approach to ecosystem conservation, offering a deeper insight into the assembly processes of bryophyte communities, particularly in fragmented forests and across diverse environmental gradients (Oishi and Yoshitaka 2016; Henriques et al. 2017) and under nonnative tree phorophyte impacts. Moreover, bryophytes demonstrate significant variability in functional traits in response to environmental changes, highlighting their adaptive capacity (Souza et al. 2020). Nevertheless, the influence of functional diversity, particularly in the context of nonnative tree species, remains largely understudied. Whether invasive tree species contribute to functional diversity in a manner comparable to or distinct from that of native trees remains an open question, with notable challenges for assessing their impact and potential role in biodiversity conservation and ecosystem functioning.

Due to the lack of previous evidence on the impact of nonnative tree species on epiphytic bryophyte diversity, we investigated the role of various phorophyte species, both native and invasive. Our study focused on early-successional forests that have spontaneously regenerated on post-agricultural landscapes near the Białowieża Primeval Forest, examining their influence on epiphytic bryophyte communities. Our study included two native (*Quercus robur* and *Acer platanoides*) and two invasive tree species (*Acer negundo* and *Prunus cerasifera*). While all four phorophytes differed in crown structure and bark morphology, they also revealed the prominent differences in mean bark pH (Table 1), as determined through our initial observations (Suppl. material 1). Identifying these differences allowed us to formulate the following hypotheses: (i) the effect of tree diameter at breast height (*DBH*) on the diversity of epiphytic bryophytes will differ amongst two native and two invasive tree species; (ii) different mechanisms of bryophyte community assembly rules will prevail on nonnative compared to native phorophytes and (iii) nonnative tree species will differ in trajectories of epiphytic bryophyte communities succession, expressed by a DBH gradient.

Materials and methods

Invasive tree species studied

Acer negundo is an invasive species in Europe, associated with temperate regions and revealing a broad ecological tolerance to diverse environmental conditions. Although frequently classified as a pioneer species (Tickner et al.

2001), it displays moderate shade tolerance, allowing it to persist under a variety of light regimes (Niinemets 1998). *Acer negundo* is a fast-growing tree species with a comparatively brief lifespan, commonly attaining an age of up to 75 years, though individuals may occasionally persist for as long as a century. In relatively open habitats, *A. negundo* develops a broad, open crown and may adopt a shrubby growth form. By contrast, under competitive conditions within forest stands, it tends to form a straighter, single-stemmed trunk. The bark is shallowly fissured and characterised by the highest mean pH and water capacity from the tree phorophytes studied (Table 1).

Prunus cerasifera is a deciduous shrub or small tree typically reaching heights up to 10 meters. It exhibits an upright, bushy growth habit and forms a broad, spreading crown. The branching is dense and intricate, with fine, and occasionally spiny, twigs. *Prunus cerasifera* may create favourable conditions for light-demanding species by developing a broad, relatively open canopy structure. The bark of *P. cerasifera* is initially smooth and with age, it develops vertical fissures and ridges, and may flake into thin scales. The bark itself is relatively hard, thin, and exhibits low roughness and limited water capacity (the lowest from the phorophyte species studied; Table 1), thereby restricting moisture availability for bryophytes. An additional characteristic of ecological relevance is its mean low pH (the lowest from the phorophyte species studied; Table 1), which may support colonisation by species typically associated with more nutrient-poor bark substrates. This nonnative tree is notably tolerant of drought conditions (Popescu and Caudullo 2016).

Native tree species studied

Two native tree species (i.e. *Q. robur* and *A. platanoides*) selected for this study reveal considerable variation in microhabitat conditions, including bark chemistry, surface texture formation, water-holding capacity, and growth rate. These traits create diverse bark microhabitats that facilitate colonisation by various ecological groups of epiphytes (Barkman 1958; Łubek et al. 2020a; Wysocki et al. 2023).

Within temperate mixed deciduous forests, *Q. robur* serves as a dominant canopy species, playing a key structural and ecological role for epiphytes (van Herk 2001; Mežaka et al. 2008; Łubek et al. 2020a; Wierzcholska et al. 2024b). As the tree matures, the central trunk often becomes indistinct within the crown, giving rise to a network of irregular, contorted limbs. The bark is grey and deeply fissured, forming robust, rectangular plates, and is characterised by relatively low mean water capacity and a close-to-neutral pH (Table 1), which significantly influences the composition and structure of epiphytic species assemblages (Barkman 1958; van Herk 2001).

Acer platanoides is typically found in moderately moist and fertile sites within temperate mixed-deciduous forests. Its stem is straight but supports horizontally oriented branches that contribute to a broad, densely foliated crown, which casts deep shade on the surrounding understory (Caudullo and de Rigo 2016). The bark displays distinct age-related variation: it is smooth and greyish-brown in younger trees, becoming darker and shallowly fissured with age, forming a reticulate pattern of narrow ridges. We found that the bark of *A. platanoides* was sub-alkaline and with relatively low water capacity (Table 1), thus shaping the composition of specific epiphytic communities (Barkman 1958; Mežaka et al. 2012; Fojcik et al. 2017).

Table 1. Descriptive statistics of pH and water capacity of bark estimated for the tree phorophytes studied. For the bark sampling protocol and raw data, see Suppl. material 1.

Tree species	pH				Water capacity			
	Mean	Max	Min	SE	Mean	Max	Min	SE
Q. robur	5.26	6.55	4.79	0.16	1.02	1.33	0.75	0.05
A. platanoides	6.05	7.32	5.44	0.17	0.90	1.24	0.64	0.06
A. negundo	7.24	7.55	6.83	0.06	1.49	1.74	1.21	0.05
P. cerasifera	4.59	4.87	3.89	0.09	0.83	1.12	0.59	0.05

Study area and study design

Our research was conducted in the northern part of the Białowieża Clearing, situated between the village of Białowieża – the largest settlement within the Polish part of the Białowieża Forest and the Białowieża National Park (Fig. 1). This region has a long history of mowing, pasturing and agricultural use, dating back to the 17th and 18th centuries, but all management forms significantly declined in the second half of the 20th century, with abandonment accelerating in the early 1990s. Today, the landscape of this area is a diverse mosaic comprising abandoned fields, mesic meadows, and pastures, along with early successional stages of oak-hornbeam forest (Tilio-Carpinetum). The forest vegetation is characterised by spontaneously regenerated stands of native *A. platanoides*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Carpinus betulus*, *Q. robur*, *Tilia cordata*, and invasive *A. negundo* and *P. cerasifera*, where the latter two can locally dominate the shrub and tree layer.

For the study, we selected 25 sample trees for each of the four phorophyte species surveyed with a similar range of diameter at breast height ranging from 9.7 to 32.5 cm. Each surveyed tree was treated as a separate, independent sampling unit (i.e. sample tree). All epiphytic bryophytes were surveyed along the tree trunk, from the very base up to 2 m above the ground. The abundance of each bryophyte species was assessed for the entire accessible trunk surface for each sampling tree, using a four-point ordinal scale: 0 – absent, 1 – low abundance (up to 3 occurrences within the sampling area), 2 – intermediate abundance (4–10 occurrences), and 3 – high abundance (more than 11 occurrences). The taxonomic nomenclature of bryophytes followed Hodgetts et al. (2020).

Epiphyte diversity parameters

We assessed the taxonomic diversity of epiphytic bryophytes by calculating species richness for each plot. We examined the functional diversity of epiphytes by choosing five cardinal functional traits representing the bryophytes' competitive abilities and adaptations to environmental stress and disturbances (Hill et al. 2007; Hodgetts et al. 2020; van Zuijlen et al. 2023): mean shoot size [mm], mean spore diameter [μm], life strategy (six classes), life form (7 classes), and growth form (acrocarpous, foliose, pleurocarpous, and thalloid; Suppl. material 2). We described the ecological preferences of epiphytic bryophyte species based on ecological indicator values (hereinafter *EIV*) established by Ellenberg et al. (1992) and Simmel et al. (2021), concerning light availability, substrate moisture, substrate nutrients content, and reaction (reflecting the species' requirements for substrate acidity; Suppl. material 2). These indicators are, to some extent, the representation of the ecological niche of each species, shaped by the combined effects of environmental

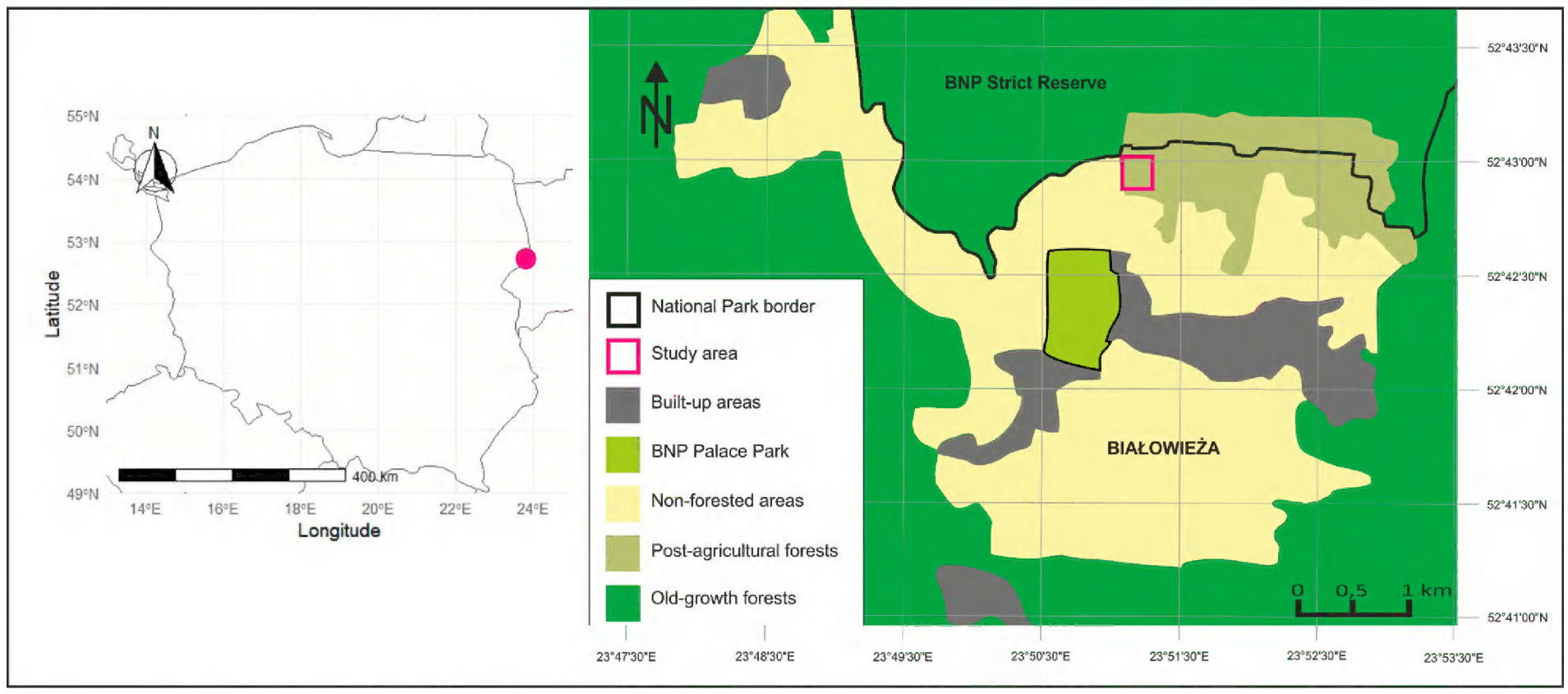

Figure 1. Study site location in the north part of the Białowieża Clearing in the surroundings of the Strict Reserve of the Białowieża National Park (*BNP*). Datum: WGS 84 (EPSG: 4326).

gradients (Smart and Scott 2009). *EIV*s serve as expert-derived indicators of the ecological niche of each species, evaluated by vegetation ecologists and frequently applied to infer ecological niches in the absence of direct instrumental measurements (Diekmann et al. 2014; Boch et al. 2019; Peppler-Lisbach et al. 2020). Although their ordinal and expert-based nature introduces certain limitations, comparisons with instrumental data have demonstrated their reliability in reflecting species' environmental preferences (Dzwonko 2001; Szymura et al. 2014).

Several functional traits and *EIV*s for epiphytic bryophytes were missing (Suppl. material 3). Rather than removing these missing values from analyses, we employed the phylogenetic imputation based on the random forest approach implemented in the "missForest::missForest()" function (Stekhoven and Bühlmann 2012; Penone et al. 2014). With the imputed dataset, we computed the community-weighted mean values (hereinafter *CWM*) for continuous traits and *EIV*s, using the species abundance as a weighting factor. Considering categorical traits, we calculated the percentage contribution of each category within each plot, weighted by the species abundance. In further analyses, we used only the categories represented by the values higher than 0 in at least 70% of plots. Thus, for the life strategy, we considered the percentage contribution of species exhibiting the colonist and perennial strategies. For the life form, we included species with turf and acrocarpous life forms, while for the growth form, we focused on species with the pleurocarpous growth form.

Using the imputed functional trait dataset and the "FD::dbFD()" function (Laliberté and Legendre 2010; Laliberté et al. 2014), we calculated three metrics of bryophyte *FD* for each sample tree: functional richness (*FRic*), functional dispersion (*FDis*), and functional divergence (*FDiv*). *FRic* quantifies the extent to which species' trait combinations fill niche hyperspace and the diversity of their realized niches within an assemblage (Hedberg et al. 2014). Low *FRic* values may indicate that bryophytes utilize a low volume of the niche hyperspace, implying a strong influence of environmental filtering in shaping the community assembly processes, often associated with pioneer habitats or stressful and extreme habitat conditions (Grime 2006). Alternatively, low *FRic* values may suggest that epiphytes utilize

a large volume of the niche hyperspace but have low diversity in their realized ecological niches within the assemblage, indicating a prevalence of interspecific competition in shaping the community assembly processes (Mayfield and Levine 2010). In contrast, high *FRic* values may suggest that a large volume of the available niche hyperspace is occupied by functionally diverse species, reflecting a substantial role of niche differentiation in determining the functional composition of the species assemblages (Villéger et al. 2008; Busch et al. 2019; Łubek et al. 2020b; Czortek et al. 2021; Czortek et al. 2023). *FDis* quantifies the dissimilarities in the composition of species' functional traits within a community, represented by the mean distance of each species from the centroid of the trait hyperspace (Hedberg et al. 2014). *FDiv*, compared to *FDis*, measures the average degree of dissimilarity between species' traits and the central point of the occupied niche space. As a result, *FDiv* is more sensitive to species with extreme trait values, which can help highlight the role of pioneer, rare, or specialized species in shaping community structure (Mason et al. 2005; Villéger et al. 2008; Pla et al. 2012; Czortek et al. 2023). Low *FDis* and *FDiv* values may indicate the dominance of species with trait values close to the centroid, suggesting that environmental filtering plays a central role in structuring species assemblages. This may occur when few species are present in low abundances or when a small number of species with high abundances dominate, leading to interspecific competition (Grime 2006; Mayfield and Levine 2010; Czortek et al. 2021). Conversely, high values of *FDis* and *FDiv* may reflect higher functional dissimilarities among species, indicating that niche differentiation is likely the primary driver of species coexistence within the community (Tilman et al. 1997; Carroll et al. 2011; Łubek et al. 2020b; Czortek et al. 2021; Czortek et al. 2023).

To account for the dependence of functional diversity metrics on species richness, we computed their standardised effect sizes (*SES*), which represent the deviation of each metric from the expected value under the null model (Gotelli 2000). We generated null models by randomly assembling communities across 999 permutations of community data matrices using the independent swap algorithm, which preserves both species' occurrence frequencies and the overall species richness of each sample. *SES* were calculated following the methodology presented by Czortek et al. (2021). In this framework, extreme *SES* values indicate that the observed metrics are significantly higher or lower than what would be expected by chance as expressed by the null model generated for particular species richness.

Data analysis

We performed all statistical analyses employing R software (version 4.3.0, "Already Tomorrow"; R Core Team 2023). To assess the effect of tree species host, *DBH*, and interaction between the tree species identity and *DBH* on species composition of epiphytic bryophytes, we used a Canonical Correspondence Analysis (CCA) ordination implemented in the "vegan::cca()" function (Oksanen et al. 2025). We evaluated the statistical significance of these effects using a PERMANOVA analysis, as implemented in the "vegan::anova.cca" function (Oksanen et al. 2025).

We employed linear regression techniques to identify the main drivers influencing bryophyte species richness, three components of functional diversity *SES*, *CWM*s of two continuous functional traits and four *EIV*s, as well as the percentage contributions of epiphytes with colonist and perennial life strategies, turf and

acrocarpous life forms, and pleurocarpous growth form. We considered tree species identity, *DBH*, and the interaction between tree species and *DBH* as key predictors of epiphytic bryophyte vegetation characteristics, including them in each of the 15 models constructed. To mitigate biases related to the underdispersion of the response variable, we used a generalised linear model with a Conway-Maxwell-Poisson distribution to assess the species richness of bryophytes, implemented in the "glmmTMB::glmmTMB()" function (Brooks et al. 2017). We chose this approach based on a very low dispersion parameter value (*disp* = 0.25; $P < 0.001$) indicated by the dispersion test conducted with the "DHARMa::testDispersion()" function (Hartig 2025). To examine the *SES* of functional diversity metrics, as well as the *CWM*s of continuous functional traits and *EIV*s, we used linear models, assuming that the response variables followed a near-normal distribution. To account for differences in the proportion of epiphytic bryophytes representing specific life strategies, life forms, and a selected growth form, we employed generalised linear models with a beta distribution for the response variables ("glmmTMB::glmmTMB()" function; Brooks et al. 2017). We evaluated the models using Akaike's Information Criterion corrected for small sample size (*AICc*), comparing the *AICc* values of each model with that of a null (intercept-only) model.

In evaluating the significance and visualising the results of the models, we focused more on effect sizes rather than P-values. This choice stems from the fact that *P*-values are highly sensitive to sample size, and relying solely on them can result in biologically significant patterns being misinterpreted as not significant (Wasserstein and Lazar 2016). To assess the effect sizes of *DBH* and the interaction between tree host species identity and *DBH*, we presented the results of the models using marginal responses, which represent predicted values with all other explanatory variables held constant (using the "ggeffects::ggpredict()" function; Lüdecke 2025). For visualizing the effect sizes of tree host species identity, we computed marginal means for each model and applied the Tukey post hoc test with studentized adjustment for multiple comparisons implemented in the "emmeans::emmeans()" function (Lenth 2025).

Results

We recorded 42 species of epiphytic bryophytes on all four phorophyte tree species. We identified substantial differences in the species composition of epiphytic bryophytes, with the first and second ordination axes (CCA1 and CCA2) explaining 41.32% and 27.31% of the variance in species assemblage dissimilarities, respectively (Fig. 2). The most pronounced effects were attributed to tree host species ($\chi^2 = 1.32$; $F = 10.94$; $P = 0.001$) and the interaction between *DBH* and tree host identity ($\chi^2 = 0.17$; $F = 1.41$; $P = 0.038$), while *DBH* alone ($\chi^2 = 0.06$; $F = 1.51$; $P = 0.06$) had a comparatively weaker influence on bryophyte species composition. We identified *A. negundo* and *Q. robur* as the most compositionally heterogeneous, while sample trees representing *P. cerasifera* and *A. platanoides* were the most homogenous in regards to epiphyte species composition. For most species, we revealed strong affinities to specific tree hosts, while only a low number of bryophytes, located in the centre of the ordination plot, revealed no clear association with a particular host.

The parameters of all models performed for each characteristic of epiphytic bryophyte vegetation are presented in Suppl. material 4. The mean bryophyte richness was the highest in sample trees representing *P. cerasifera* (7.9 ± 0.3 SE taxa) compared to the three remaining phorophytes surveyed (Fig. 3A). An individual effect of

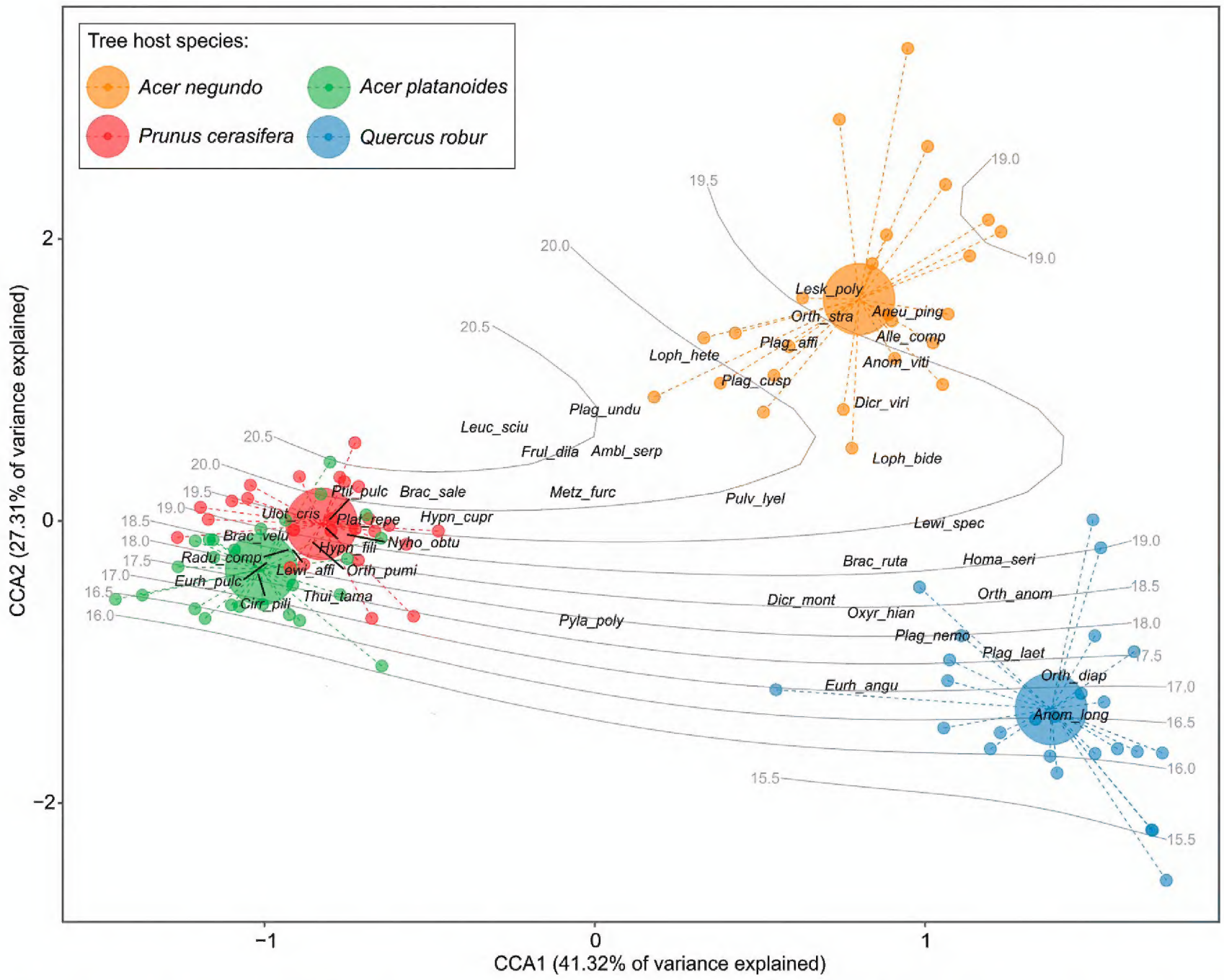

Figure 2. Visualization of a Canonical Correspondence Analysis ordination assessing the effect of tree species host, diameter at breast height, and interaction between the tree species host and diameter at breast height on species composition of epiphytic bryophytes. Small points represent the coordinates of sample trees representing particular tree host species. Large points represent centroids of species composition of epiphytic lichens in sample trees. Grey isolines represent diameter at breast height [cm]. Black labels represent the species coordinates in ordination space: Alle_comp – *Alleniella complanata*, Ambl_serp – *Amblystegium serpens*, Aneu_ping – *Aneura pinguis*, Anom_long – *Anomodon longifolius*, Anom_viti – *A. viticulosus*, Brac_velu – *Brachytheciastrum velutinum*, Brac_ruta – *Brachythecium rutabulum*, Brac_sale – *B. salebrosum*, Cirr_pili – *Cirriphyllum piliferum*, Dicr_mont – *Dicranum montanum*, Dicr_viri – *D. viride*, Eurh_pulc – *Eurhynchiastrum pulchellum*, Eurh_angu – *Eurhynchium angustirete*, Frul_dila – *Frullania dilatata*, Homa_seri – *Homalothecium sericeum*, Hypn_cupr – *Hypnum cupressiforme*, Hypn_fili – *H. filiforme*, Lesk_poly – *Leskea polycarpa*, Leuc_sciu – *Leucodon sciuroides*, Lewi_affi – *Lewinskya affinis*, Lewi_spec – *L. speciosa*, Loph_bide – *Lophocolea bidentata*, Loph_hete – *L. heterophylla*, Metz_furc – *Metzgeria furcate*, Nyho_obtu – *Nyholmiella obtusifolia*, Orth_anom – *Orthotrichum anomalum*, Orth_diap – *O. diaphanum*, Orth_pumi – *O. pumilum*, Orth_stra – *O. stramineum*, Oxyr_hian – *Oxyrrhynchium hians*, Plag_affi – *Plagiomnium affine*, Plag_cusp – *P. cuspidatum*, Plag_undu – *P. undulatum*, Plag_laet – *Plagiothecium laetum*, Plag_nemo – *P. nemorale*, Plat_repe – *Platygyrium repens*, Ptil_pulc – *Ptilidium pulcherrimum*, Pulv_lyel – *Pulvigera lyellii*, Pyla_poly – *Pylaisia polyantha*, Radu_comp – *Radula complanata*, Thui_tama – *Thuidium tamariscinum*, Ulot_cris – *Ulota crispa*.

DBH on species richness was marginally positive (Fig. 3B). While in *A. negundo* and *A. platanoides* plots the species richness increased slightly, in sample trees representing *P. cerasifera* it increased from 7.03 to 9.25 taxa at *DBH* ranging from 9.7 to 32.5 cm (Fig. 3C). The mean *FRic SES* was the highest in *P. cerasifera* and *A. platanoides* (0.47 ± 0.19 SE and 0.43 ± 0.18 SE, respectively), compared to sample trees representing *A. negundo* and *Q. robur* (Fig. 3D). A single effect of *DBH* on *FRic SES* was similarly weak as compared to *A. negundo* and *Q. robur* (Fig. 3E, F). In *P. cerasifera* and *A. platanoides* sample trees, *FRic SES* decreased from 1.29 and 1.06 to –0.59 and –0.38, respectively, at *DBH* ranging from 9.7 to 32.5 cm (Fig. 3F). We identified *A. platanoides* and *P. cerasifera* as having the highest values of *FDis SES* (0.47 ± 0.14

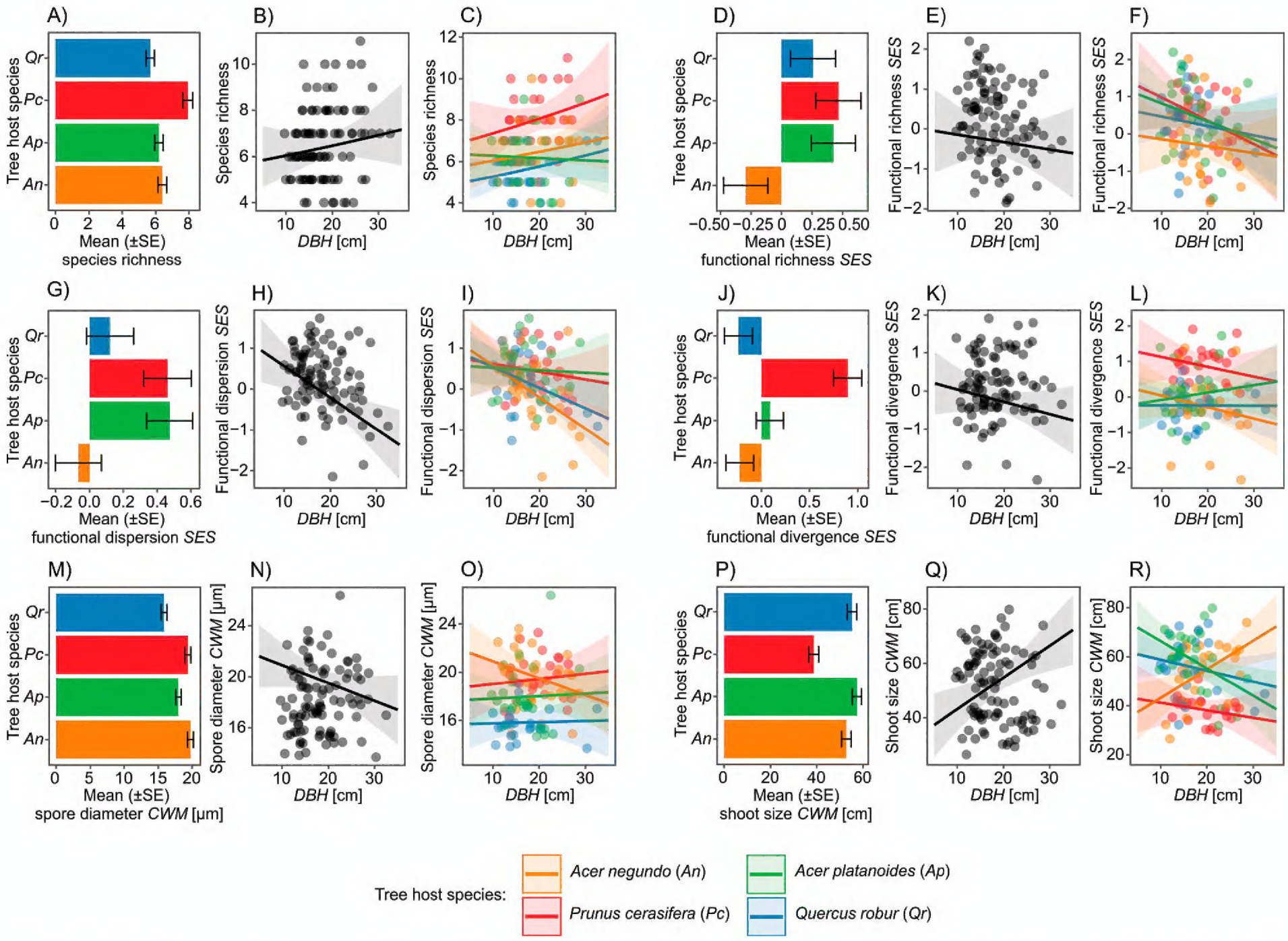

Figure 3. Partial regression plots visualising results of linear models (note generalised linear model with a Conway-Maxwell-Poisson distribution to assess the species richness) testing for effects of tree host species, tree diameter at breast height, and interaction between tree host species and tree diameter at breast height (*DBH*) on bryophyte: species richness (**A–C**), standardized effect size (SES) of functional richness (**D–F**), functional dispersion SES (**G–I**), functional divergence SES (**J–L**), and community weighted means (*CWM*) of spore diameter (**M–O**) and shoot size (**P–R**). For model parameters see Suppl. material 4.

SE and 0.46 ± 0.14 SE, respectively), compared to *A. negundo* and *Q. robur* sample trees (Fig. 3G). A single effect of *DBH* on *FDis SES* was strongly negative, revealing a decrease from 0.95 at 9.7 cm to –1.36 at 32.5 cm (Fig. 3H). While for sample trees representing *P. cerasifera* and *A. platanoides*, the values of *FDis SES* decreased slightly, for *A. negundo* and *Q. robur* they decreased prominently from 0.95 and 0.78 to –1.36 and –0.73, respectively, at *DBH* ranging from 9.7 to 32.5 cm (Fig. 3I). We identified *P. cerasifera* as the tree host having the highest mean *FDiv SES* (0.90 ± 0.15 SE), compared to the three remaining hosts (Fig. 3J). A slight decrease in *FDiv SES* with increasing *DBH* corresponded to gentle declines in these metric values observed for *P. cerasifera* and *A. platanoides* sample trees (Fig. 3K, L).

The mean spore diameter *CWM* did not differ considerably among the four tree hosts studied (Fig. 3M), but it decreased prominently with increasing *DBH*, from 21.6 µm at 9.7 cm to 17.4 µm at 32.5 cm (Fig. 3N). While the mean spore diameter *CWM* in regards to *A. negundo* decreased in the same range as found for the single effect of *DB*H, no influence of *DBH* was observed for the other tree hosts (Fig. 3O). The *CWM* of mean shoot size showed no notable differences across the four tree hosts examined, but it increased notably with increasing *DBH* from 37.3 mm at 9.7 cm to 72.3 mm at 32.5 cm (Fig. 3P, Q). This relationship followed that identified for

A. negundo, where the values of this *CWM* increased in the same range as found for a single effect of *DBH* (Fig. 3R). For the remaining tree hosts, the effect of *DBH* on the mean shoot size *CWM* was negative, with the largest decrease identified for *A. platanoides* sample trees, declining from 71.9 mm at 9.7 cm to 38.5 mm at 32.5 cm of *DBH*.

The mean proportion of colonists was the highest in *A. platanoides* (49.2 ± 3.0% SE), compared to the three remaining hosts studied (Fig. 4A). A single effect of *DBH* on the percentage of colonists was similarly negligible as revealed for *A. negundo*, *P. cerasifera*, and *Q. robur* sample trees (Fig. 4B, C). Regarding *A. platanoides*, the fraction of colonists decreased considerably from 75.0% at 9.7 cm to 19. 0% at 32.5 cm of *DBH* (Fig. 4C). We identified *A. negundo* and *Q. robur* phorophytes as having the highest mean proportion of perennials (75.4 ± 3.4% SE and 73.2 ± 3.2% SE, respectively), compared to *P. cerasifera* and *A. platanoides* (Fig. 4D). We observed a notable positive increase in the perennials' fraction with increasing the *DBH* from 44.0% at 9.7 cm to 95.0% at 32.5 cm (Fig. 4E). This trend mirrored the significant increases in the proportion of perennials with *DBH* reported for *A. negundo* and *A. platanoides* (from 44.0 and 23.0% at 9.7 cm to 95.0% and 66.0% at 32.5 cm, respectively), with slight decreases observed for *P. cerasifera* and *Q. robur* (Fig. 4F). The percentage of turf bryophytes was relatively consistent across all four tree hosts surveyed (Fig. 4G). While the single effect of *DBH* on turf epiphytes was barely negative, for *P. cerasifera*, this effect was strongly positive (increasing from 47.0% at 9.7 cm to 98.0% at 32.5 cm; Fig. 4H, I). In *A. platanoides* sample trees, the fraction of turf bryophytes decreased gently with increasing the *DBH*, while for *A. negundo* this effect was marginally positive (Fig. 4I). We identified *Q. robur* and *A. platanoides* as having the highest mean percentage of acrocarpous epiphytes (40.4 ± 2.5% SE and 38.0 ± 2.4% SE, respectively), compared to *P. cerasifera* and *A. negundo* (Fig. 4J). We observed a notable positive decrease in the proportion of acrocarpous epiphytes with increasing the *DBH* from 31.0% at 9.7 cm to 16.0% at 32.5 cm (Fig. 4K). This pattern followed the prominent decrease in the acrocarpous epiphytes' contribution with *DBH* for *A. platanoides* (from 51.0% at 9.7 cm to 23.0% at 32.5 cm), while for the remaining tree hosts, this relationship was weaker (Fig. 4L). The fraction of pleurocarpous bryophytes was relatively similar across all four tree hosts surveyed, but it increased considerably alongside increasing the *DBH* from 30.0% at 9.7 cm to 84.0% at 32.5 cm (Fig. 4M, N). While in *P. cerasifera* the proportion of pleurocarpous bryophytes decreased from 64.0 to 41.0%, in sample trees representing *A. negundo* it increased from 30.0% to 84.0% as *DBH* ranged from 9.7 to 32.5 cm, with only slight positive effects found for *A. platanoides* and *Q. robur* (Fig. 4O).

The individual effects of tree host species on all four *CWM*s of *EIV*s analysed were relatively weak (Fig. 5A, D, G, J). The values of the light *EIV CWM* remained constant as *DBH* increased (Fig. 5B). Regarding *P. cerasifera*, the light *EIV CWM* values increased markedly from 5.8 at 9.7 cm to 6.7 at 32.5 cm of *DBH*, while for remaining tree hosts, we observed negative but milder effects of tree size (Fig. 5C). A strong negative influence of *DBH* on the moisture *EIV CWM* (a decrease from 4.4 at 9.7 cm to 3.8 at 32.5 cm) reflected the negative impacts of *DBH* reported for all four tree hosts surveyed (Fig. 5E, F), with the largest effect reported for *A. negundo* (in the same range as found for single effect of *DBH*; Fig. 5F). At *DBH* ranging from 9.7 to 32.5 cm, the *CWM* values of substrate nutrients content *EIV* increased from 5.0 to 5.9 (Fig. 5H). However, in *A. platanoides*, these values decreased substantially from 6.7 to 5.4. In sample trees representing *A. negundo* and *Q. robur*, the *CWM* values of substrate nutrients content *EIV* increased slightly,

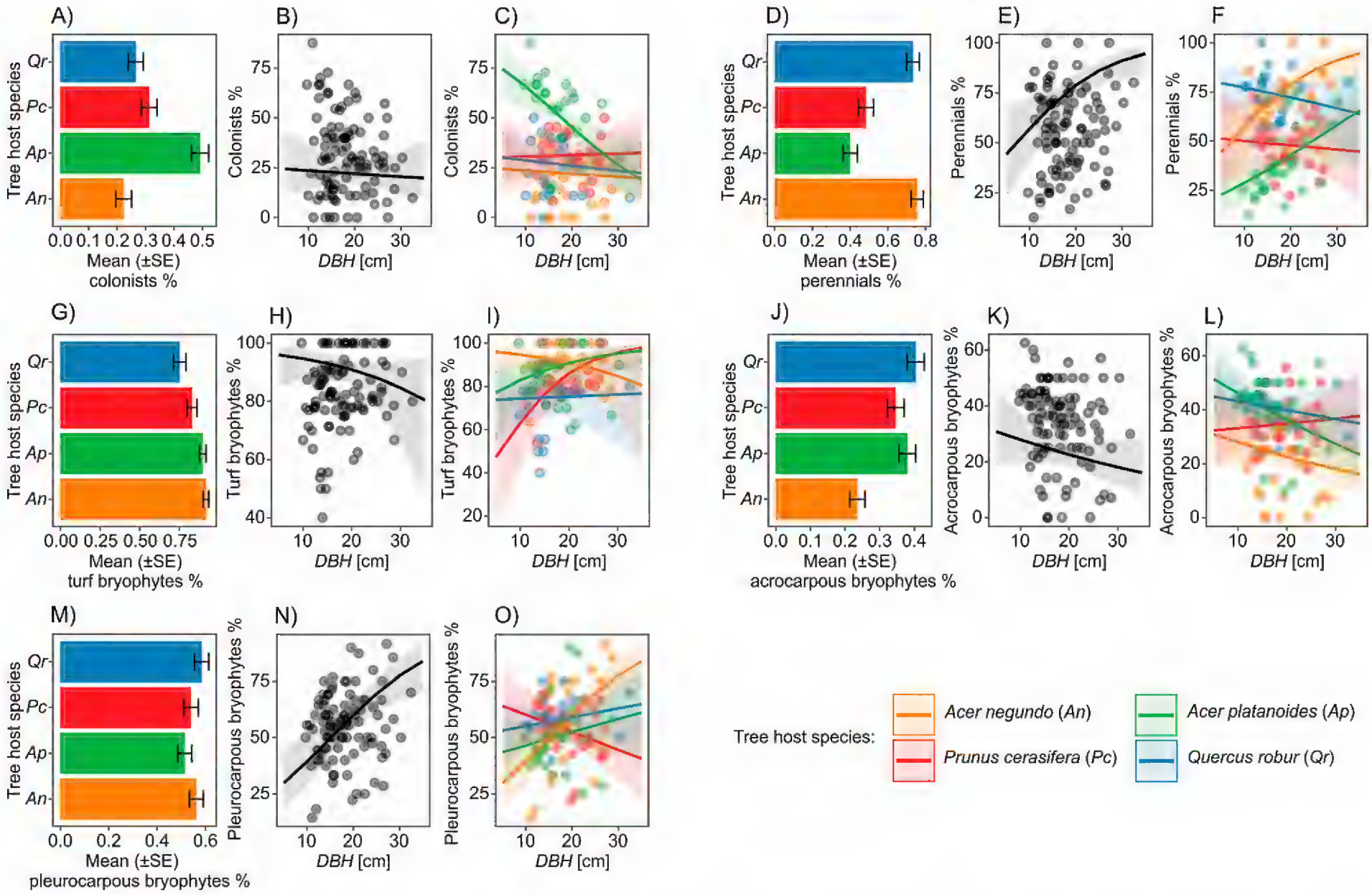

Figure 4. Partial regression plots illustrating the results of generalized linear models with a beta distribution of the response variables assessing the effects of tree host species, tree diameter at breast height (*DBH*), and their interaction on the percentage contribution of colonist (**A–C**), perennial (**D–F**), turf (**G–I**), acrocarpous (**J–L**), and pleurocarpous (**M–O**) bryophytes on sample trees surveyed. Note the zero–inflation effects in the case of colonists and acrocarpous bryophytes proportion. For model parameters see Suppl. material 4.

while no distinct effect of *DBH* was observed for *P. cerasifera* (Fig. 5I). The *CWM* values of reaction *EIV* increased from 5.7 at 9.7 cm to 6.7 at 32.5 cm of *DBH* (Fig. 5K). While in case of *A. negundo* these values increased in the same range as found for single effects of *DBH*, in *P. cerasifera* they decreased from 6.1 to 5.4 at *DBH* ranging from 9.7 to 32.5 cm. Considering *A. platanoides* and *Q. robur*, the effect of *DBH* on reaction *EIV CWM* was negligible (Fig. 5L).

Discussion

Epiphyte community assembly processes on *A. negundo*

Substantially large dissimilarities in epiphyte species composition correspond with opposite effects of *DBH* on functional diversity parameters revealed for *A. negundo* and *A. platanoides*. However, comparable ecological mechanisms could influence the structure of epiphyte assemblages on both phorophytes. A negative relationship between *DBH* and functional richness *SES* in *A. platanoides*, along with a negative influence of tree size on functional dispersion *SES* in *A. negundo*, may suggest that interspecific competition is a predominant ecological mechanism shaping epiphyte community assembly on both hosts. However, the varying impacts of *DBH* on bryophyte functional traits and *EIV*s may suggest that different processes contributed to reducing the role of habitat filtering while strengthening the importance of interspecific competition regarding these phorophytes.

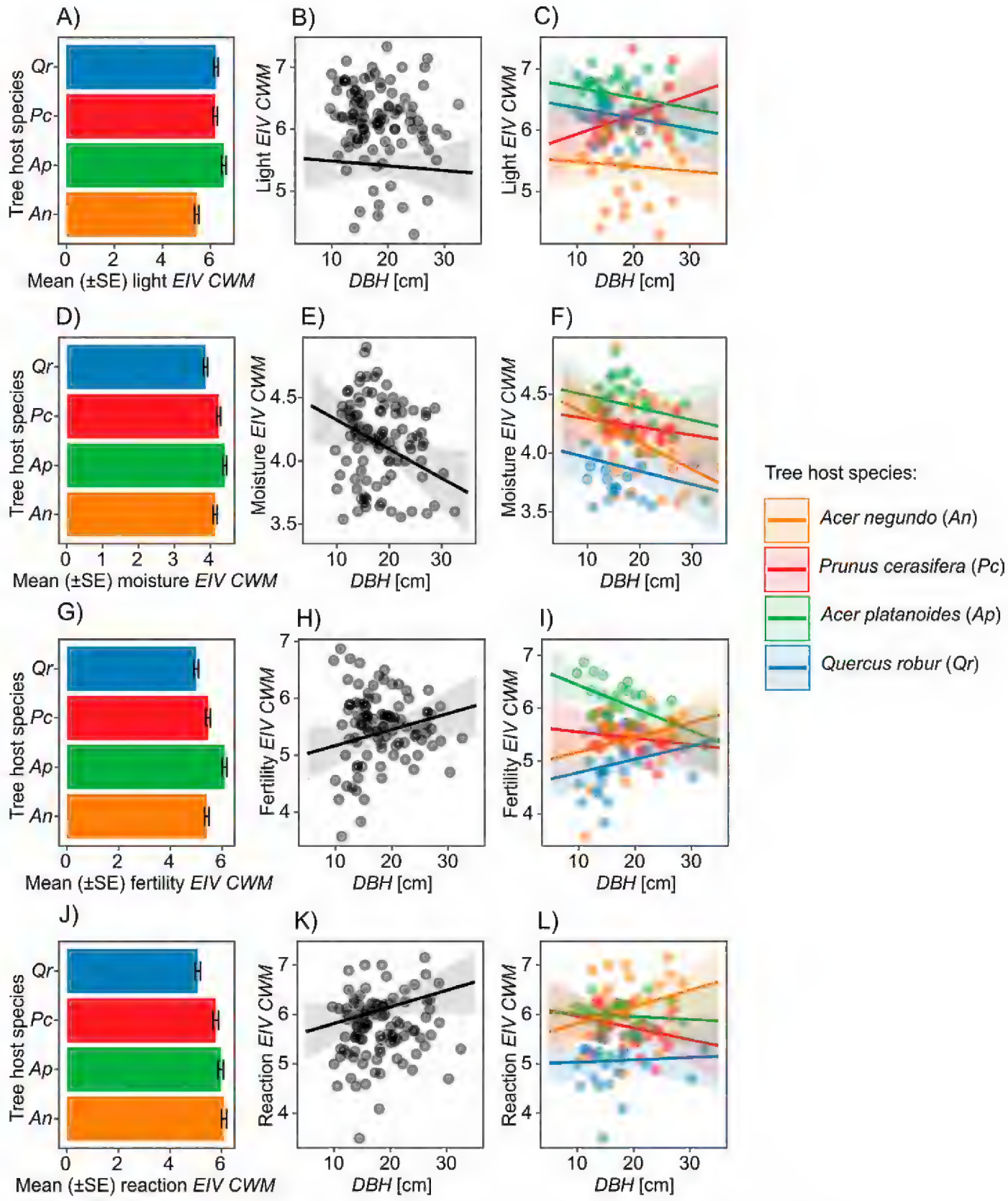

Figure 5. Partial regression plots visualizing the results of linear models predicting the influence of tree host species, tree diameter at breast height (*DBH*), and their interaction on community weighted means (*CWM*) of bryophyte ecological indicator values (*EIV*): light *EIV* (**A–C**), substrate moisture (**D–F**), substrate nutrient content (**G–I**), and substrate reaction (**J–L**). For model parameters see Suppl. material 4.

Regarding *A. negundo*, we demonstrated that with increasing *DBH*, the proportion of perennial species of high bark nutrient and pH demands, forming large-size plagiotropic mats, increased, while the proportion of turf and acrocarpous epiphytes decreased. This pattern corresponds with the highest mean pH recorded for *A. negundo*, compared to the other three phorophytes studied. Moreover, we noticed that the proportion of species with small spores also decreased with increasing tree size. This can be attributed to the increasing proportion of competitive species on larger *A. negundo* trees, which form large mats, and are typical of permanent habitats without disturbances (During 1992). This phenomenon is representative of tree hosts with fertile and highly water-absorbent bark, as well as limited sunlight.

The lack of decrease in the proportion of light-demanding colonists may suggest that a small fraction of pioneers and acrocarpous bryophytes could persist on large *A. negundo* trees in the upper parts of the canopy. These taxa may cope

well with moderate sunlight in the upper canopy, which may be compensated by the highest mean water capacity of bark, compared to the remaining tree species studied. Therefore, functional richness *SES* did not change with increasing *DBH* as the degree of trait hyperspace filled by the realized niches of species could remain high on large *A. negundo* individuals. However, functional dispersion *SES* and the dissimilarities between the realized niches of epiphytes decreased drastically with increasing *DBH*. This phenomenon can be linked with the fact that most functionally dissimilar species could be replaced rapidly by competitors, which would dominate because of their high abundances, and thus filling almost completely the entire niche hyperspace in the more shaded parts of *A. negundo*'s trunks.

Acer negundo, growing in early successional stages of oak-hornbeam forest with other native trees, seems to resemble native phorophytes such as *A. platanoides* – a typical component of mature mixed-deciduous forests (Fudali and Szymanowski 2019; Wierzcholska et al. 2024b). Its relatively high ability to host bryophytes, indicative of ancient forests, may be linked to the similarly high mean bark pH observed for *A. platanoides*, as well as a substantially relatively higher water capacity of bark, compared to *A. platanoides*. This clearly points *A. negundo* as a similarly favourable host for epiphytic bryophytes as revealed for its native counterpart (Mitchell et al. 2021). However, it should be noted that the presence of ancient forest indicator bryophytes on *A. negundo*'s bark may be influenced by the close surroundings of the Białowieża Primeval Forest. Nevertheless, this highlights the potential of *A. negundo* as a host for epiphytes with the highest conservation priority.

Coexistence patterns of bryophyte species on *A. platanoides*

The proportion of colonists and acrocarpous epiphytes decreased with increasing *DBH* of *A. platanoides* but the contribution of pleurocarpous perennials increased. In addition, the diversity of niches realized by epiphytes decreased with increasing the tree size, indicated by lower functional richness *SES* on larger *A. platanoides* trees. This may suggest that epiphytes associated with early successional stages could be unable to compete with faster-growing perennials on *A. platanoides* trees with larger *DBH*. Indeed, pleurocarpous perennials form bigger and more stable mats, reveal broader ecological amplitudes, and demonstrate higher abilities for interspecific competition than acrocarpous colonists. The bark of *A. platanoides* provides favourable microhabitat conditions, including slow exfoliation, relatively early furrowing, and higher pH. Despite one of the lowest water capacities, compared to other tree phorophytes studied, the relatively early formation of bark fissures may, to some extent, support moisture retention, providing favourable conditions for this functional group of epiphytes. These bryophytes are typically associated with later stages of bryophyte assemblage succession, reaching the highest abundance particularly at the base of the trunk (Cieśliński et al. 1996; Mežaka and Kirillova 2019; Wierzcholska et al. 2024b). Similar results were obtained by Martins et al. (2024), who reported the highest proportion of plagiotropic bryophytes in laurel forests, which provide stable microclimatic conditions for this epiphyte functional group, including high humidity, moderate temperatures, and low microclimatic fluctuations.

The functional dissimilarities between the bryophyte realized niches remained high on *A. platanoides* with larger *DBH*, expressed by a lack of a more pronounced relationship between functional dispersion *SES* and *DBH*. This phenomenon can be attributed to the continued presence of pioneers and colonists forming small-

sized mats (i.e. turf bryophytes), as well as taxa associated with neutral or lower pH of bark. These functional groups of species could persist on trees with larger *DBH*, particularly in the upper and more sun-exposed parts of the trunk, which are likely to exhibit lower bark pH compared to the more fertile lower trunk sections, as indicated by the high mean bark pH recorded there. Therefore, with increasing *DBH* on *A. platanoides*, the role of habitat filtering in shaping epiphyte community assembly may diminish relative to interspecific competition, yet it may remain notably important in the upper parts of the trunk. In this context, epiphyte assemblages inhabiting the bark of *A. platanoides* may demonstrate relatively similar rules of community assembly to those reported for trees in the Strict Reserve of the Białowieża National Park (Wierzcholska et al. 2024b). Additionally, epiphytes considered indicators of ancient forests were also present on larger *A. platanoides* trees, including more shade-tolerant species and taxa producing smaller sizes.

Mechanisms shaping the epiphyte functional composition on *P. cerasifera*

The high similarities of epiphyte species composition revealed for *P. cerasifera* and *A. platanoides* correspond with similar effects of *DBH* on their functional diversity parameters. While functional richness *SES* increased alongside increasing *DBH*, we did not observe more pronounced effects of tree size on functional dispersion *SES* in the case of both phorophyte species. This may suggest that interspecific competition could be of the highest importance in determining the structure of epiphyte assemblages, as we demonstrated for *A. platanoides*. However, the lack of complementarity between the effects of *DBH* on epiphyte functional traits and *EIV*s indicates that mechanisms other than competition may play a more important role in shaping epiphyte community assembly processes on *P. cerasifera* trees.

While the proportion of turf bryophytes on *P. cerasifera* increased, as it did on *A. platanoides*, the contribution of pleurocarpous epiphytes decreased with increasing *DBH*. Furthermore, contrary to *A. platanoides*, on *P. cerasifera* the percentage of light-demanding species grew with increasing tree size. Moreover, on larger *P. cerasifera* trees, more species were forming smaller-size mats. Therefore, the role of habitat filtering in explaining the community assembly processes on *P. cerasifera* with larger *DBH* may be of high importance. Confirmation of these patterns may be found in the similarly high functional dispersion *SES* (indicating high functional dissimilarities between epiphytes) on larger *P. cerasifera* trees compared to smaller ones. This may be explained by the wide occurrence of numerous pioneer species, promoted by substantially low bark pH and water capacity.

One may expect that larger *P. cerasifera* trees could be colonized by more competitive species, as reflected in the negative relationship between *DBH* and functional richness *SES*. However, this lower diversity of epiphyte realized niches may indicate the onset of colonization of larger *P. cerasifera* trees by light-demanding species. Despite being colonists, these taxa could perform better in the more sun-exposed canopy than bryophytes with larger mats belonging to perennial species. Because in the highly insolated upper parts of the trunk, both bark pH and water-holding capacity may be even lower than in the more basal parts – sections already characterized by high acidity and low water absorbency – these species can exert negative impacts on other bryophytes typically associated with larger trees. In this regard, *P. cerasifera* may demonstrate substantial similarity to trees composing the inten-

sively managed forests dominated by nonnative tree hosts, such as *R. pseudoacacia* (Jagodziński et al. 2018; Mišíková and Mišík 2024). Moreover, it seems that *P. cerasifera* may resemble trees in urban parks, where the trunks are dominated by light-demanding nitrophilous colonists (Pokorny et al. 2006; Fudali 2012). Thus, due to specific bark properties and canopy structure, the bryophyte assemblages forming on mature *P. cerasifera* trees seem to be completely different compared to the native phorophyte species of the Białowieża Primeval Forest (Cieśliński et al. 1996; Wierzcholska et al. 2024b).

The role of epiphytes associated with later stages of bryophyte assemblage succession may be of similar importance as revealed for pioneers in maintaining the functional dissimilarities between the epiphyte realized niches on *P. cerasifera* with a larger *DBH*. The highest functional divergence on *P. cerasifera* (regardless of *DBH*) may support this idea, which can be interpreted as a simultaneous effect of the presence of numerous pioneers and the colonization by epiphytes associated with mature oak-hornbeam forest. Nevertheless, both groups of taxa appear to be bryophytes with realised niches that significantly differ from those of the other species observed on *P. cerasifera*. Thus, while light-demanding species may increase their ecological success due to their occurrence in the extensive and loose canopy – where bark pH and water capacity are presumably lower than in the lower trunk sections – bryophytes inhabiting the basal part of the trunk may benefit from the shading, which could help offset the relatively low water capacity we observed.

Mechanisms shaping the epiphyte community assembly processes on *Q. robur*

Regarding *Q. robur*, we identified a similarly negative effect of *DBH* on functional dispersion *SES* as reported for *A. negundo*, with a corresponding lack of influence of tree size on functional richness *SES*. This may hint at a prevalence of similar ecological mechanisms in shaping the epiphyte communities structure on both phorophytes, with interspecific competition likely to exert the biggest effects. However, large dissimilarities in species composition of bryophytes reported between these tree hosts, as well as opposite effects of *DBH* on selected epiphyte functional traits and *EIV*s, contradict this idea.

The proportion of acrocarpous and perennial epiphytes producing relatively large stems, and the contribution of light-demanding species was lower on larger *Q. robur* trees. The loss of these species can be attributed to changes in bark structure on trees with larger *DBH*, which begins to peel over time, potentially affecting the disappearance of suitable microhabitats for the taxa mentioned above. This, in turn, may lead to higher functional similarities between species, expressed by the decrease in functional dispersion *SES* alongside an increase in *DBH*. On this basis, one would expect that the importance of interspecific competition would be higher on larger *Q. robur* trees. However, we observed that functional richness *SES* did not change with the host *DBH*. This may be attributed to the similarly high volume of the trait hyperspace filled by the similarly high diversity of the species realized niches, both on small and large *Q. robur* trees. One possible explanation of this pattern may be partial replacement of functionally dissimilar bryophytes (mostly pioneers) by more functionally similar plagiotropic epiphytes and taxa of higher bark nutrient demands, as supported by the close-to-neutral bark pH

recorded. Additionally, more functionally dissimilar species typical of mature forests at the same time could become a substantial part of the epiphyte assemblages developing on *Q. robur*. Therefore, it is tempting to conclude that most of the other analysed bryophyte functional traits and *EIV*s remained unchanged by *DBH*, which may be considered a signal of the so-called "functional turnover" of the species' realised niches taking place in the *DBH* gradient of *Q. robur* trees.

We demonstrated that *Q. robur* trees had bark with relatively low water capacity, which could promote the appearance of pioneer species. However, as the tree increases its *DBH* and the bark structure changes, with small cracks evolving into larger fissures, both competitors and mature forest epiphytes could start to colonize the bark of *Q. robur*, as this newly formed structure may increase their ecological success. At the same time, some colonists could still persist on larger *Q. robur* trees, likely due to legacy effects connected with the maintenance of some pioneer microhabitats. Nevertheless, we assume that for *Q. robur*, compared to the other tree hosts surveyed, changes in epiphyte functional diversity depending on *DBH* were the least pronounced. This can likely be attributed to its growth rate, substantially slower than the other host trees. Thus, *Q. robur* may act as a host where bryophyte assemblage succession could be of the slowest rate among the four phorophytes studied.

Conclusions

This study presents the first evaluation of the impact of invasive tree species on the functional diversity of epiphytic bryophytes and is one of the few investigations examining the effects of invasive trees on bryophyte species richness. By examining the mechanisms shaping species and functional diversity of bryophytes for native and nonnative phorophytes in early-successional temperate deciduous forests, we evaluated the impact of these trees on epiphytic bryophyte communities. Although interspecific competition may play a key role in shaping epiphyte community assembly on larger *A. negundo* and *A. platanoides*, both tree species supported functionally diverse bryophyte communities. This has been evidenced by their relatively high capacity to colonise by both pioneer and late-successional or ancient forest indicator species. Moreover, we revealed a comparable high capacity to host epiphytes with contrasting functional traits for invasive *P. cerasifera* and native *Q. robur*. We showed different trajectories of the impact on epiphytic bryophyte community assembly of two studied nonnative tree species, highlighting the lack of a universal scheme of impact. These effects were tree species-specific, indicating low transferability of impact inference from a single species. Therefore, future studies on the effects of nonnative trees on epiphytes should cover a wider range of tree species, and include functional diversity assessment. Both nonnative tree species may emerge as phorophytes with notable potential for supporting the restoration and persistence of high bryophyte species and functional diversity. At the same time, they may act as effective refuges and important sources of propagules for bryophytes living on trees in forest monocultures, urban landscapes, and other human-altered ecosystems. Understanding the mechanisms that influence the species and functional diversity of epiphytic bryophytes on nonnative tree species can be valuable for conservation planning and the development of forest management strategies under global environmental changes.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

PC: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing; MKD: Formal analysis, Visualization, Writing – original draft, Writing – review & editing; AŁ: Conceptualization, Writing – original draft, Writing – review & editing; MTM: Investigation, Writing – review & editing; SW: Conceptualization, Investigation, Data curation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing

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Data availability

The collected material is deposited in the Wrocław University of Environmental and Life Sciences. Raw data are deposited in the Białowieża Geobotanical Station and are available on request.

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Supplementary material 1

Raw data on bark pH and water capacity (WC) of the studied tree phorophytes

Authors: Patryk Czortek, Marcin K. Dyderski, Anna Łubek, Marcin T. Mazurkiewicz, Sylwia Wierzcholska

Data type: pdf

Explanation note: WC – water capacity of bark.

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Link: https://doi.org/10.3897/neobiota.100.154929.suppl1

Supplementary material 2

Characteristics of the ecological indicator values and functional traits of epiphytic bryophytes

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Supplementary material 3

Ecological indicator values (EIVs) and functional traits of epiphytic bryophytes used in this study, their ranges, standard deviation (SD) and completeness

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Supplementary material 4

Parameters of model estimates testing for different effects

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Data type: pdf

Explanation note: Parameters of model estimates testing for effects of tree host species (Tree), tree diameter at breast height (DBH), and interaction (marked in table by colons) between tree host species and tree diameter at breast height on bryophyte vegetation characteristics. For host tree species (Tree) A. negundo is a reference level (intercept values). AICc – AICc of full model; AICc0 – AIC of null (intercept-only) model; SES – standardized effect size; CWM – community weighted mean; EIV – ecological indicator value. Statistically significant results are in bold.

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